

## **Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction**

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### **ABSTRACT**

Two key factors in a population's risk of extinction are major population declines induced by natural or anthropogenic events (catastrophes) and whether the population's rate of growth increases or decreases at very low abundance levels. These two elements should be included in any population viability analysis (PVA), but estimates of the frequency and intensity of catastrophic events and data on the dynamics of low population densities are difficult to obtain. We examined the literature on population dynamics of otariids (fur seals and sea lions), to determine how frequently populations are subjected to major population declines, and to what extent depleted populations recover from low population size. We present frequency distributions for percentage declines for otariid life-stages (pup, juvenile, adult female and male), and describe eight examples of events leading to a population decline of 50% or greater among otariids. We found that numerous otariid populations have been reduced to very low densities by exploitation (low enough to be thought extinct) and have recovered to levels where they are no longer at risk of extinction. This suggests that the reduction in population rate of increase at low densities in otariid populations may not be strong.

*Keywords:* catastrophes, otariids, population viability, population rate of increase, population decline, depensation, exploitation

### **INTRODUCTION**

Extinction can occur as a result of a chronic, gradual decline of a population or as a result of short-term catastrophic events. Most extinction models include environmental and demographic stochasticity, and model these processes through variation in fecundity, birth or survival rates (Belovsky, 1987). Catastrophes, such as droughts, fires, El Niño events, epidemics, invasion by a new competitor or predator, or human alteration of the environment, have the potential to cause sudden major reductions in population size in short time periods and are an important factor in calculations of extinction risk (Menges, 1990; Lande, 1993; Mangel & Tier, 1994). Indeed, Menges (1990), studying an endangered plant, concluded, 'catastrophic mortality dominates estimates of population viability'. Mangel & Tier (1994) reviewed catastrophic events in a broad range of taxonomic groups and concluded that catastrophes 'may be more important in determining persistence time than any other factor usually considered'. Yet it is trivially demonstrated in the literature that catastrophic events will dominate the stochastic components of birth and death processes in affecting population dynamics and risk

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of extinction. Thus, a prerequisite to a realistic calculation of extinction risk is an analysis of the frequency and intensity of catastrophic events.

Catastrophic events can most easily be thought of as mortality events leading to a reduction in population size, and could be considered the extreme of normal stochastic survival relationships. However, we find it more convenient to consider catastrophic events as independent of stochastic survival; indeed, we suggest that it is generally more important to consider such catastrophes than it is to include minor year-to-year changes in survival. Catastrophes can be thought of as recruitment failures or long-term declines in abundance. For purposes of calculating extinction risk it matters little if the population was subjected to a one time 70% mortality event, or declined 70% over a number of years. Indeed, for the purpose of this paper we will include any major decline in abundance as a 'catastrophe', recognizing that this may be due to a discrete environmental perturbation such as an El Niño event, or a less discrete decline in abundance over a number of years that is unexplained. We will specifically exclude harvesting since it is not an unpredictable environmental event, and is (in theory) controllable by management agencies. Using our approach, data on population-level effects of harvesting could be used in estimates of extinction risk as a separate parameter based on expected harvest rates for species of concern.

Extinction risk is normally calculated within a population viability analysis that consists of a set of equations relating changes in population abundance to natural and anthropogenic changes (Gilpin & Soulé, 1986; Boyce, 1992). To incorporate catastrophic events into a PVA formally we must specify how frequently they occur and how much of the population declines as a result; these numbers, in turn, should be obtained by examination of the historical record for related species. In this paper we will show how the frequency and intensity of catastrophic events can be determined for a single taxonomic group – the otariids. This work is, to our knowledge, the first attempt to evaluate the entire published literature for a taxonomic group to evaluate the risk of catastrophic population declines.

The risk of extinction of marine mammals, and particularly otariids, is of considerable conservation concern. Otariid species, which demonstrate polygyny and metapopulation dynamics, are particularly vulnerable to catastrophic events. Several populations are currently listed under the US Endangered Species Act (ESA) and the IUCN Red List of Threatened Animals. Under the ESA, the western stock of Steller's Sea Lions is currently listed as endangered, and the eastern stock of Steller's Sea Lions and the Guadalupe Fur Seal are listed as threatened. The Steller's Sea Lion is also listed as endangered by the IUCN, and the Galapagos, Juan Fernandez, Guadalupe, and Northern Fur Seals as well as the Hooker's and Galapagos Sea Lions, are listed as vulnerable.

Despite the risks faced by these otariid populations, there has been little effort to quantify the frequency of catastrophic events. Geraci *et al.* (1982) and Menges (1990) attempt to quantify the frequency of catastrophic events for specific types of catastrophes (pneumonia in Harbor Seals (*Phoca vitulina*), and weather impacts on a population of lousewort). We have found no other attempts to estimate the frequency or intensity of catastrophic events. Most models of pinniped population dynamics do not incorporate catastrophic stochasticity. We examine the published population data of otariids to determine how frequently populations are subjected to catastrophic population declines.

A second important concern in PVA is the dynamics of populations at low densities. If birth and survival rates stay constant or increase at lower densities (compensation) then the risk of extinction is clearly lower than if birth and survival rates decrease at low densities (depensation). This topic too is almost universally ignored within PVAs, and a pseudo-extinction population level is adopted as an indicator of extinction. It would clearly be pre-

ferable to include depensation in the PVA, and recent work (Myers *et al.*, 1995; Liermann & Hilborn, 1997) has established a methodology for using historical data from other populations to estimate the parameters of depensation formally as an input into PVA. While conducting a review of the literature on pinnipeds, we also note cases where populations were reduced to very low numbers and how the populations responded. The data provide a basis for considering possible levels where depensation might act.

Any analysis of population dynamics should attempt to survey the historical literature on the taxonomic group of concern and quantify both catastrophic events and dynamics at low densities. We believe that the approach adopted here for otariids could be applied to other taxonomic groups in analysis of extinction risk.

## MATERIALS AND METHODS

A literature search was conducted to prepare a database on the frequency and intensity of catastrophic events and periods of low population abundance for otariids (summarized in Tables 1–4, Fig. 1). In total, 89 documents were reviewed (published between 1825 and 1997). Of these, 25 included data adequate to quantify the impact of catastrophic events and known extinction thresholds for otariids.

The phocids (true seals) were not considered in the study because it was thought that their distinct life history (e.g. phocids exhibit less marked sexual dimorphism in size, have adult sex ratios of 1:1, and are solitary breeders) would probably translate into markedly different responses to catastrophic events and low population densities than those of otariids.

### Historical data on extinction thresholds

To document known extinction thresholds for otariids, the following were recorded for each species/stock: number of years of data on trend or population size, lowest population size,

**Table 1.** Summary of literature that suggest extinction thresholds for otariids. For each population, the date of presumed extinction and apparent recovery, and factors influencing population status are reported

Population	Status	Date	Event/Cause
Guadalupe Fur Seal	Presumed extinct	1928	Directed harvest
<i>Arctocephalus townsendi</i>	Vulnerable (IUCN)	1994	Population recovered to 7408 animals
Juan Fernandez Fur Seal	Presumed extinct	1917	Directed harvest
<i>A. townsendi</i>	Vulnerable (IUCN)	1993	Population recovered to 18 000 animals
Antarctic Fur Seal	Near extinction	1933	Directed harvest
<i>A. gazella</i>	(many local extinctions)		
	Not listed	1996	Population recovered to 1 600 000
Subantarctic Fur Seal	Near extinction	1810	Directed harvest
<i>A. tropicalis</i>	Not listed	1982	Population recovered to 305 000 adults
New Zealand Fur Seal	Near extinction	1830	Directed harvest
<i>A. forsteri</i>		1990	recovered to 135 000 animals
Japanese Sea Lion	Extinct	Early 1900s	Directed harvest
<i>Zalophus californianus japonicus</i>	Extinct (IUCN)	1997	Possible that some exist on remote islands of Sea of Japan or Russia.
Cape Fur Seal	Near extinction	Late 1800s	Directed harvest
<i>A. pusillus</i>		1993	Population recovered to 1 700 000

**Table 2.** Documented catastrophic declines of otariids (>50% decline, either in one year or over an extended period). Eight examples of catastrophic events have been documented in the literature; this value is used as a numerator in equation 1 to determine the range for probability of catastrophe

Population	Cause and Effect
Northern Fur Seal (San Miguel Island) <i>Callorhinus ursinus</i>	<b>El Niño:</b> 50% decline of adult females in 1983; 20% decline of adult males in 1983; 60% decline in pups born in 1983; 50% decline in pups born in 1984; 40% decline in pup growth rate in 1983; 25% decline in pup growth rate in 1984; local redistribution
Northern Fur Seal <i>C. ursinus</i>	<b>Unknown:</b> 55% decline of population between 1973 and 1988 (St. George Island)
Galapagos Fur Seal <i>A. townsendi</i>	<b>El Niño:</b> 100% pup mortality in 1980, 1981 and 1982 cohorts; 'partial' loss of 1979 cohort; 100% adult male mortality in 1982; at least 30% adult female mortality in 1982–83; 89% decrease in number of pups born in 1983; foraging trips 3 times longer and more variable; slow recovery
Galapagos Sea Lion <i>Z.c. wollebaeki</i>	<b>El Niño:</b> >50% decline of juveniles in 1982; 100% pup mortality in 1982; 'reduced' no. pups born in 1983; 100% mortality of 1982 cohort; slow recovery
South American Fur Seal <i>A. australis</i>	<b>El Niño:</b> >41% pup mortality in 1982; 'increase' in adult mortality in 1982; 50% decrease in pup growth rate in 1983– increased foraging trips in 1982–83; local redistribution in 1982–83
South American Sea Lion (Falkland Islands)	<b>Unknown:</b> 93% decline of population between 1937 and 1965
South American Sea Lion (Argentine coast) <i>Otaria byronia</i>	<b>Unknown:</b> 90% decline of population between 1938 and 1975
Steller's Sea Lion <i>Eumetopias jubatus</i>	<b>Unknown:</b> 64% decline of population between 1952 and 1996 (western stock)

current status, cause of the decline, dates over which this decline occurred, and the source of the information (Tables 1–4).

To distinguish local extinction from population-level extinction, in cases where the degree of population subdivision was unknown, local extinctions were documented but not used in

**Table 3.** Summary of historical population data for otariids for which data are adequate to detect a >50% annual decline, and number of years of data available for each. For each population, the timeframe and maximum number of years of monitoring, and the type of data, are indicated. The sum of the maximum number of years of monitoring data is 377; this value is used as a denominator in equation 1 to determine the upper bound for annual probability of catastrophe

Population	Time period for data considered adequate to detect a >50% decline	Total years for which a >50% decline was likely to have been detected	Type of data	Reference
Northern Fur Seal (Pribilof Islands)	1912–24 1968–97	41	Annual pup counts	Loughlin <i>et al.</i> (1994)
Juan Fernandez Fur Seal	1985–93	8	Periodic pup counts	Hubbs & Norri 1971; Wickens & York, 1997
Northern Fur Seal (San Miguel Island)	1972–97	25	Annual pup counts	DeLong & Antonelis, 1991, Melin <i>et al.</i> (1996)

Table 3. *Continued*

Population	Time period for data considered adequate to detect a >50% decline	Total years for which a >50% decline was likely to have been detected	Type of data	Reference
Guadalupe Fur Seal	1954–97	43	Periodic pup counts	Barlow <i>et al.</i> , 1997, Peterson <i>et al.</i> (1968)
Galapagos Fur Seal	1976–85	9	Behavioural, annual pup counts	Trillmich, 1987, Trillmich & Ono, 1991
Cape Fur Seal	1971–93	22	Periodic pup counts	Shaughnessy (1987); Wickens, 1994, Butterworth <i>et al.</i> , 1995, Wickens & York, 1997
Antarctic Fur Seal (S. Shetland Islands, S. Georgia)	1966–91	25	Periodic pup counts	Bengston <i>et al.</i> , 1990, Boyd, 1993
Antarctic Fur Seal (Macquarie Island)	1954–86	32	Periodic pup counts	Shaughnessy <i>et al.</i> , 1988a
Antarctic Fur Seal (Heard Island)	1963–93	20	Periodic pup counts	Shaughnessy <i>et al.</i> 1988b, Shaughnessy & Goldsworthy, 1993
New Zealand Fur Seal	1988–93	5	Periodic pup counts	Shaughnessy <i>et al.</i> , 1988a, Wickens & York, 1997
Steller's Sea Lion (Western stock)	1960–97	37	Annual pup counts	NMFS, 1995
Steller's Sea Lion (Eastern stock)	1960–97	37	Annual pup counts	Barlow <i>et al.</i> , 1997
California Sea Lion (US stock)	1972–97	25	Annual pup counts	Barlow <i>et al.</i> , 1997
California Sea Lion (Western Baja California stock)	1979–1991	12	Annual pup counts	LeBoeuf <i>et al.</i> , 1983; Aurioles & LeBoeuf, 1991, Lowry <i>et al.</i> , 1992
California Sea Lion (Gulf of California stock)	1979–87	8	Annual pup counts	Zavala, 1990; Lowry <i>et al.</i> 1992
Galapagos Sea Lion	1976–85	9	Annual pup counts	Trillmich, 1987, Trillmich & Ono, 1991
South American Sea Lion	1983–88	5	Behavioural, mark-recapture	Majluf, 1991
South American Fur Seal	1983–88	5	Behavioural, mark-recapture	Majluf, 1991
Australian Sea Lion	1987–92	5	Annual pup counts; behavioural	Gales <i>et al.</i> , 1992; Reijnders <i>et al.</i> , 1993, Higgins 1993
New Zealand Sea Lion (South New Zealand Islands)	1992–96	4	Periodic pup counts	Cawthorn (1993); Gales & Fletcher 1996
Total		377		

our calculations for extinction threshold. This approach was taken to assure that emigration was not mistaken for extinction.

#### Historical data on catastrophic events for otariids

All data referring to natural catastrophic events of various magnitudes were recorded (see Tables 2–5, Fig. 1). We tabulated all recorded population declines, but were primarily interested in the frequency and intensity of major population declines. As an example, in this paper we focus on catastrophes that result in greater than a 50% decline, although any particular threshold level could be chosen. The probability of catastrophic events for each species may be calculated based on the number of populations with adequate data to detect a catastrophe, the number of years of data for each population, and the number of populations affected by each level of catastrophe. Specifically, the annual probability of a catastrophic event ( $p$ ) can be estimated as:

$$p = \frac{N}{\sum_i Y_i} \quad (1)$$

where  $N$  is the number of catastrophic events observed, and  $Y_i$  is the number of years and populations observed closely enough to have detected a catastrophic event, had it occurred.

If there were annual counts of each population it would be straightforward to tabulate the frequency of catastrophic events of different sizes; however, in many cases we have only occasional counts of the population. If we observe 1000 animals in one year and 10 years later observe that the population is still 1000 animals, can we say that the population has not suffered a 50% (or any level) mortality event during this period? We used the following rules: we assumed that the maximum rate of annual increase was 12% per year, which corresponds to the average of the maximum growth rates for known pinnipeds (Barlow *et al.*, 1995). Thus, if a population was measured at an initial time ( $N_t$ ) and again  $n$  years later ( $N_{t+n}$ ), and there was a 50% decline at some time during those  $n$  years, then

$$N_{t+n} = 0.5N_t(1.12)^n \quad (2)$$

The ratio of ( $N_{t+n}$ ) to ( $N_t$ ) for  $n = 1, 2, 3, 4, 5, 6$  is 0.56, 0.63, 0.70, 0.79, 0.88, 0.99. Thus, we could say that if we find two similar counts 6 years apart there could have been a 50% mortality event between counts. Allowing a 20% factor for demographic stochasticity and measurement error in the counting process, we assume 4 years as the time between similar counts for which we can say with confidence that a 50% mortality event between the counts would have been detected. In cases where there are more than 4 years between the two counts, but the second count is significantly higher, we can use the same rules to determine whether we can be confident that there was no 50% mortality event in between. This simple rule could be modified for other levels of catastrophic events; for instance if we had chosen a 30% mortality event then we would simply change the 0.5 in equation 2 to 0.3. The use of the 20% factor is conservative and we are probably overestimating the frequency of 50% catastrophies, by reducing the denominator of equation 2.

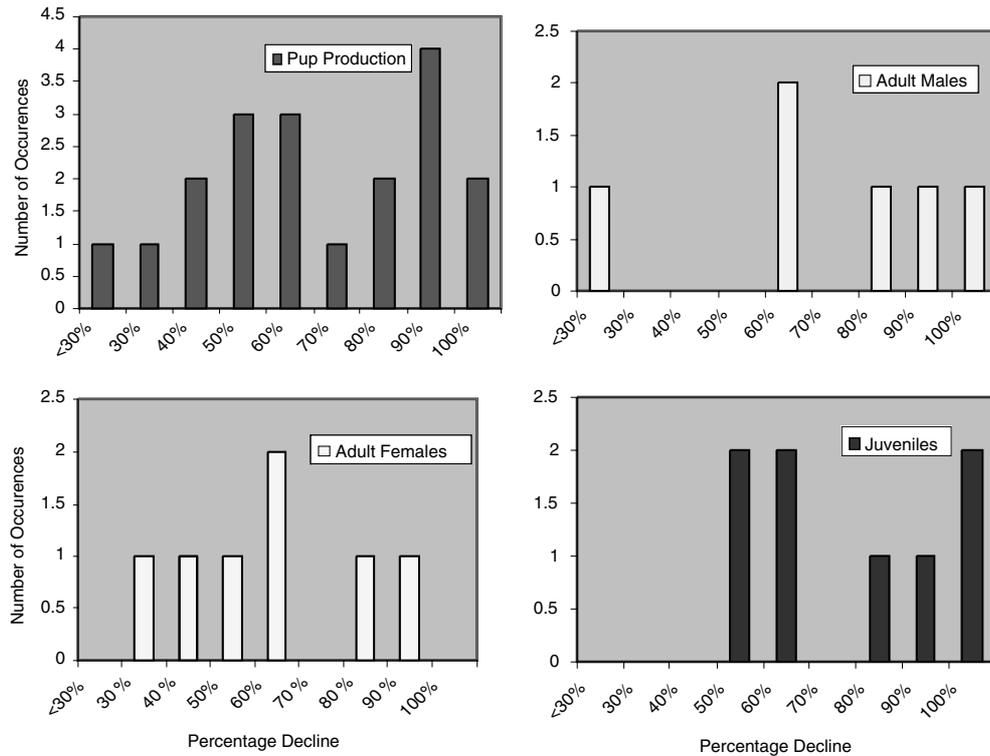
## RESULTS

#### Historical data on extinction thresholds

Seven populations of otariids were found, at one time or another, to have declined to critically low numbers (i.e. likely less than a few hundred; Table 1). Identification of a general extinction threshold for otariids was difficult, however, because six of these populations

**Table 4.** Summary of historical population data for otariids. For each population, the timeframe and maximum number of years of monitoring, and the type of data, are indicated. The sum of the maximum number of years of monitoring data is 3237; this value is used as a denominator in equation 1 to determine the lower bound for annual probability of catastrophe

Population	Time frame for available data	Max. number of years of monitoring	Type of data
Northern Fur Seal (Pribilof Islands)	1786–1997	211	Harvest data; annual pup counts since 1968
Northern Fur Seal (San Miguel Island)	1968–97	29	Annual pup counts since 1972
Juan Fernandez Fur Seal	1792–1993	205	Harvest data; sporadic population estimates
Guadalupe Fur Seal	1808–1997	189	Harvest data; sporadic population estimates; periodic pup counts since 1954
Galapagos Fur Seal	1808–1997	189	Sporadic population estimates
Cape Fur Seal	1687–1997	310	Harvest data; sporadic population estimates
Antarctic Fur Seal (S. Shetland Islands, S. Georgia)	1820–1997	177	Harvest data; sporadic population estimates; periodic pup counts
Antarctic Fur Seal (Heard Island)	1855–1997	142	Harvest data; sporadic population estimates; periodic pup counts
Antarctic Fur Seal (Macquarie Island)	1810–1997	187	Harvest data; sporadic population estimates; periodic pup counts
Subantarctic Fur Seal	1810–1997	187	Harvest data
New Zealand Fur Seal	1810–1997	187	Harvest data; sporadic population estimates
Steller's Sea Lion (Western stock)	1952–97	45	Annual pup counts since 1960
Steller's Sea Lion (Eastern stock)	1952–97	45	Annual pup counts since 1960
California Sea Lion (US stock)	1969–97	28	Annual pup counts since 1975
California Sea Lion (Western Baja California stock)	1979–97	18	Annual pup counts 1979–91
California Sea Lion (Gulf of California stock)	1979–97	18	Annual pup counts 1979–87
Japanese Sea Lion	1900–97	97	Sporadic population estimates
Galapagos Sea Lion	1808–1997	189	Annual pup counts conducted 1981–85
South American Sea Lion	1930–97	67	Harvest data, sporadic population estimates, behavioural, mark–recapture studies conducted since 1983
South American Fur Seal	1515–1997	482	Harvest data, sporadic population estimates, behavioural, mark–recapture studies conducted since 1983
Australian Sea Lion	1953–97	44	Harvest data; sporadic population estimates
New Zealand Sea Lion (South New Zealand Islands)	1806–1997	191	Harvest data; sporadic population estimates; periodic pup counts in portion of range since 1968
Tota		3237	



**Figure 1.** Frequency and intensity of population declines (either in one year or over an extended period) between 1930 and 1997 in pup production, number of adult females, number of adult males, and number of juveniles for the otariid species listed in Table 3.

were at one time considered extinct, but were later rediscovered. Only one population, the Japanese Sea Lion (*Zalophus californianus japonicus*), is now believed to be extinct.

Here we summarize the results of our examination of available information concerning extinction thresholds for otariids. In particular, we present, for each population, the time-frame for available data, the apparent date and cause of catastrophic decline, and the current status of the species.

#### **Guadalupe Fur Seal (*Arctocephalus townsendi*)**

Between 1808 and 1810, 130 000 fur seals were harvested; an additional 5575 animals were harvested between 1876 and 1892 (Wedgforth, 1928; Fleischer, 1987; Gallo, 1994). The Guadalupe Fur Seal was thought to be extinct in 1928 (Hubbs, 1956). The population was rediscovered in 1954 and has since then apparently increased steadily. Pup production has been estimated at 1500 annually (Gallo, pers. comm. as cited in Wickens & York, 1997). In 1987, 3259 animals were counted at Guadalupe Island and the population was estimated at 6000 animals (Gallo, pers. comm. as cited in Reijnders *et al.*, 1993). In 1993 the population was estimated at 6443 (Gallo, 1994); and in 1994 at 7408 (Barlow *et al.*, 1997). Currently the population is classified as Vulnerable by the IUCN (IUCN, 1996).

#### **Juan Fernandez Fur Seal (*Arctocephalus townsendi*)**

During the end of the 18th century and beginning of the 19th century, several million seals were harvested from the Juan Fernandez Islands (Hubbs & Norris, 1971). In 1792 approxi-

**Table 5.** Estimated frequency of catastrophic events for different probabilities of detecting an event during the historical record (from equation 3). Equation 1 is modified so that the denominator reflects parameter  $q$ , such that a catastrophe during the period of intense population monitoring would have definitely been observed, but that during other years in the recorded history there is a lower probability ( $q$ ) of observing a catastrophic event. Minimum and maximum of values for  $p$  (0.25–2.1%) below also reflect the range of catastrophe probability determined by equation 1

Probability of detecting a catastrophe during the historical record ( $q$ )	Estimated frequency of catastrophic events ( $p$ )
0.00	0.0212
0.05	0.0154
0.10	0.0121
0.15	0.0099
0.20	0.0084
0.25	0.0073
0.30	0.0065
0.35	0.0058
0.40	0.0053
0.45	0.0048
0.50	0.0044
0.55	0.0041
0.60	0.0038
0.65	0.0036
0.70	0.0034
0.75	0.0032
0.80	0.0030
0.85	0.0028
0.90	0.0027
0.95	0.0026
1.00	0.0025

mately 37 000–38 000 animals were killed, initiating the China trade (Busch, 1985). In 1801, ‘a single ship carried one million skins to the London market’ (Busch, 1985). Between 1793 and 1807 an estimated 3500 000 animals were taken (Hubbs & Norris, 1971), and by 1824 the population was approaching commercial extinction (Hubbs & Norris, 1971). By 1891, the population was estimated at approximately 300–400 animals and by 1917 the population was presumed extinct (Hubbs & Norris, 1971). Not until 1965 were residual populations on four of five islands discovered, apparently constituting the original range of the species. In 1970 the population was estimated at 752; by 1985 4700 animals were counted; and by 1990–91 the population was estimated at 12 000 (Hubbs & Norris, 1971; Francis, personal communication as cited in Wickens & York, 1997). In 1993 the population was estimated at 18 000. The species is currently listed as Vulnerable by the IUCN (IUCN, 1996).

#### **Antarctic Fur Seal (*Arctocephalus gazella*)**

While this species inhabits a vast range throughout Antarctica, the population structure of Antarctic Fur Seals is not well understood. Thus, in our attempt to quantify the probability of extinction of small populations, it is difficult to distinguish emigration from extinction (i.e. to differentiate extinction of the entire population from that of a segment of a population). As a whole, most populations of Antarctic Fur Seals were exploited to the verge of extinction by the early 1900s (Kerley, 1983a, 1983b). In 1933, the largest population of fur seals,

that on South Georgia, was thought to be extinct (Laws, 1973). In the absence of adequate data to justify assumptions about population structure of Antarctic Fur Seals, we considered the species as one population in the extinction-threshold calculation. Here we summarize the known information on extinction events for local populations of Antarctic Fur Seals.

Between 1810 and 1820 approximately 193 300 fur seals (Antarctic, Subantarctic and New Zealand species) were harvested at Macquarie Island. While the identity of the harvested fur seals is unknown, by 1850 these species were overharvested to a point of critically low numbers; 'Antarctic, Subantarctic and New Zealand Fur Seals were harvested from the time of discovery in July 1810 to near extinction' (Shaughnessy & Fletcher, 1987; Shaughnessy *et al.*, 1988a). By 1981, the population was estimated to include 800–1000 animals, and Antarctic and Subantarctic Fur Seals re-established breeding colonies.

On South Georgia, an estimated 1.2 million fur seals were harvested in 1825, which suggests that there was a substantial population before sealing began (Weddell, 1825; Bonner, 1968; Payne, 1977; Boyd, 1993). Small-scale hunting continued until 1907, when the population was thought to be extinct (Bonner, 1968; Laws, 1973; Boyd, 1993). An apparently rapid recovery has occurred since 1907, and by 1983 the population was estimated at 1600 000 animals (Boyd, 1993).

On the South Shetland Islands, 320 000 fur seals were killed between 1820 and 1822. The population was apparently 'virtually exterminated' (Weddell, 1825, O'Gorman, 1961, 1963), although the initial abundance is highly uncertain. By 1959, the first post-exploitation pups were observed (O'Gorman, 1961, 1963); by 1990, 18 881 animals were counted. Currently, it appears that the species is continuing its recovery and recolonization of rookery sites following 19th century commercial exploitation (Bengtson *et al.*, 1990).

On Heard Island, the first reported harvest occurred in 1855–56, when approximately 500 fur seals were reportedly taken (Shaughnessy *et al.*, 1988b). Although actual catch data were not reported, harvesting continued until the 1870s when fur seals were thought to be exterminated (Shaughnessy *et al.*, 1988b). Between 1947 and 1955 the maximum count of fur seals on Heard Island was 51 animals (Shaughnessy *et al.*, 1988b). The first definitive record of breeding was reported in 1963 and the population increased to 500 (1965), 3000 (1969), and 4500 (1980) animals. By 1990, 15 000 animals were estimated to occur on Heard Islands; and by 1992 a total of 21 280 animals was counted, representing the highest estimate of fur seal abundance on Heard Island (Shaughnessy & Goldsworthy, 1993, Shaughnessy *et al.*, 1998b).

#### **Subantarctic Fur Seal (*Arctocephalus tropicalis*)**

Like the Antarctic Fur Seal, population structure of Subantarctic Fur Seals is not well understood. Thus, we again considered the species as one stock for the extinction threshold calculation. Here we summarize the limited information on extinction events for local populations of Subantarctic Fur Seals.

As mentioned, fur seals (Antarctic, Subantarctic and New Zealand) were harvested to the verge of extinction at Macquarie Island by 1850. A slow recolonization occurred and in 1981 Antarctic and Subantarctic Fur Seals established breeding colonies on the Island.

Subantarctic Fur Seals were also heavily exploited on Amsterdam Island in the 1800s; by 1875 fewer than 100 animals remained (Guinet *et al.*, 1994). By 1982, the population recovered to an estimated 30 500 adults (Guinet *et al.*, 1994).

#### **New Zealand Fur Seal (*Arctocephalus forsteri*)**

The New Zealand Fur Seal was heavily exploited in the early 1800s and by 1830 the species was nearly extinct (Cumpston, 1968; Baker, 1990). The entire population recovered to an esti-

mated 135 000 animals in 1990 (Taylor, 1982; Brothers & Pemberton, 1990; Dix, 1993; Shaughnessy *et al.*, 1994; Taylor *et al.*, 1995; Harcourt & Lalas, 1995). The species is currently listed as Vulnerable by the IUCN (IUCN, 1996).

#### **Japanese Sea Lion (*Zalophus californianus japonicus*)**

The Japanese Sea Lion originally ranged along the shores of Japan and Korea, and the southern Pacific shores of Russia. To our knowledge no population surveys were done. The subspecies was subject to a long history of hunting for meat and oil, and reached extremely low numbers by the early 1900s (Nakamura, 1991). The population was considered to be virtually extinct until one sea lion was sighted in 1952; according to a Japanese newspaper, 50–60 sea lions were sighted in the same location in November 1951 (Scheffer, 1958). In 1958 Dr Fukuzo Nagasaki reported that there were ‘more than 200’ California Sea Lions in the Sea of Japan (Scheffer, 1958). Currently, the subspecies is still regarded as extinct (e.g. by IUCN, 1996); however, due to limited information about the original range of the species, it is possible that some living specimens exist on remote islands of the Sea of Japan or Russia (Nakamura, 1991). We suspect that directed harvest was the primary factor contributing to extinction, but other unreported factors could have facilitated loss of this subspecies.

#### **Cape Fur Seal (*Arctocephalus pusillus*)**

Prior to the 20th century, many colonies were heavily exploited and the abundance of Cape Fur Seals was greatly reduced (Wickens, 1994). By the end of the 19th century and the beginning of the 20th century, the overall population level of the Cape Fur Seal was very small and the population was thought to have been ‘virtually exterminated’ (Shaughnessy, 1984). Seal Island, False Bay was visited in 1687; directed harvest began in 1796 and continued until 1830 when the population was thought to be locally extinct (Shaughnessy, 1984; Wickens, 1994). Between 1830 and 1911 the Island was recolonized (Wickens, 1994) and directed harvesting was resumed at a lower rate. By 1985, 50 000–60 000 animals were estimated to inhabit Seal Island; this estimate is considered to exceed that on the first recorded visit to the island in 1687 (Wickens, 1994). By 1993, the total population of Cape Fur Seals was estimated to include 1700 000 animals (Butterworth *et al.*, 1995; Wickens & York, 1997).

#### **Historical data on catastrophic events**

The dramatic impact of El Niño on some otariid populations has highlighted the potential for short-term catastrophic impacts on otariids, and the long slow declines of the western stock of Steller’s Sea Lion and South American Sea Lion represent another type of catastrophic decline (Table 2). For the purpose of our analysis, we have combined these two into one type of catastrophic event, considered as a single one-time event reducing the abundance of all age classes by more than 50%. The key question is in estimating the probability of such an event happening, which depends primarily on how likely it is that we would have been able to detect a catastrophic event. Applying our decision rule (4 years as the maximum timeframe to detect 50% mortality event between counts), the number of population-years observed is 377 (Table 3), and we recorded eight catastrophic events, thus the annual rate of catastrophes would be 2.1%. If instead we assume that such events would have been detected at any time in the recorded history of the populations, the denominator is 3237 (Table 4) and the annual rate would be 0.25%.

Alternatively, we can assume that a catastrophe during the period of intense population monitoring would have definitely been observed, but that during other years in the recorded history there is a lower probability ( $q$ ) of observing a catastrophic event. We can thus modify equation 1 so that the denominator reflects parameter  $q$ .

$$p = \frac{N}{\sum_i J_i + \sum_i X_i q} \quad (3)$$

where  $J_i$  is the number of years during which a catastrophic event would have definitely been detected, and  $X_i$  is the number of years for the entire recorded history of the populations. The estimated frequency of a catastrophe for different values of  $q$  is shown in Table 5. For example, if we were certain that a catastrophic event would not have been detected during the historical record,  $q = 0$  and our estimated frequency would equal 2.1%. Alternatively, if we knew that an event would have been detected during the entire recorded history of the population, then  $q = 1$  and the frequency would be 0.25%. It should be noted that these bounds (0.25–2.1%) reflect the range of catastrophe probability determined by equation 1. Within this range, one could choose a probability for the parameter  $q$  and then calculate the probability distribution for the frequency of catastrophes  $p$ . This parameter,  $q$ , could be updated and refined by incorporating expert opinion regarding the likelihood of detecting a catastrophe for particular species.

The denominator of equation 3 is the most difficult component to determine due to the fact that many populations were not monitored systematically and that differences in monitoring effort between populations affect the power to detect catastrophic events. We identified 22 otariid populations for which some monitoring has occurred, and noted the type of data available (Table 4).

To calculate the maximum possible value for the denominator of equation 1, we assumed that a 50% decline in abundance would have been observed any time during the years listed in Table 4. At the other extreme, we recognize that effort and monitoring methods were highly inconsistent among the 22 populations. To calculate the minimum value for the denominator we considered those populations and years where pup counts were made at least every 4 years and any major change in abundance would definitely have been detected. For 20 of the 22 populations, the time period during which systematic counts were made was recorded (Table 3). This latter estimate of the number of years examined represents a minimum approximation and therefore encompasses the full range of catastrophes that a population might experience. We did not include the Japanese Sea Lion in our analyses because (1) virtually no population data exist for this population, and (2) there is strong evidence that the primary cause of extinction was harvesting, which would not be regarded as a catastrophic event.

Population declines of greater than 50% were documented for four populations resulting from the 1982–83 El Niño event, and for four other populations that have declined slowly over time without an obvious cause (Western stock of Steller's Sea Lion, Northern Fur Seals on St. George island, and two populations of the South American Sea Lion) (Table 2). Catastrophes of less than 50% and those that were not quantified were documented, but not included in the current calculations for probability of 50% catastrophe. Here we present for each of the otariid species the information currently available concerning the type, duration, and intensity (effect on population) of catastrophic events.

#### Northern Fur Seals (*Callorhinus ursinus*)

El Niño is a suite of anomalous oceanographic conditions occurring periodically on a global scale. In the North Pacific, El Niño often is associated with reduced upwelling, changes in sea level and sea surface temperature, and unusual storm patterns, often with a consequent reduction in water-column productivity (Trillmich *et al.*, 1991). Trillmich & Ono (1991) reported that El Niño events may cause significant population-level declines of pinnipeds.

Northern Fur Seals breeding on San Miguel Island in California experienced significant

adverse effects as a result of the 1982–83 El Niño event. Females foraged longer; juvenile mortality doubled from 1981 to 1982 and 1983; and the abundance of females declined by 50% in 1983 (due to mortality or emigration) (DeLong & Antonelis, 1991). The population experienced a 20% decline of adult males and a 60% and 50% decline in the number of pups born in both 1983 and 1984. Further, a 40% and 25% decrease in pup growth rate in 1983 and 1984, and a local redistribution (northward migration) were reported (DeLong & Antonelis, 1991).

During the same period, the 1982–83 El Niño event had a minimal effect on Fur Seals breeding on St. George Island, in the Pribilof Islands of Alaska. A 15% decrease in preweaning juvenile survival was detected (Croxall & Gentry, 1987; York, 1990, 1991; Gentry, 1991). York (1991) postulates that El Niño may benefit populations in Northern latitudes (decreased metabolic costs associated with warmer waters), and decrease survival in Southern latitudes (decreased productivity in water column).

The Pribilof Island population of Northern Fur Seals declined significantly in the 1970s and 1980s due to an unknown agent (Briggs & Fowler, 1984; York, 1990). Between 1976 and 1982, counts of Northern Fur Seal pups on St. Paul Island declined by approximately 35%; on St. George counts declined by 55% between 1973 and 1988 (York, 1990). Entanglement with marine debris, environmental change and emigration are among the possible causes for this decline. Pup production has remained relatively stable since 1983 (York & Fowler, 1992).

#### **Galapagos Fur Seal (*Arctocephalus townsendi*)**

The most severe negative impact of the 1982–83 El Niño event on pinnipeds occurred on the Galapagos Islands (Trillmich, 1985, 1987; Trillmich & Dillinger 1991). The event resulted in a 100% loss of the 1980, 1981 and 1982 cohorts, a partial loss of the 1979 cohort, a 30% loss of adult females in 1981–82, a 100% loss of adult males in 1982, and an 89% decrease in number of pups born in 1983. Foraging trips increased in duration by threefold and the variance of the duration of foraging trips increased significantly as a result of changes in prey composition (Trillmich *et al.*, 1991; Trillmich & Dillinger, 1991). The species has recovered slowly from this event, and a local redistribution (i.e. migration to better habitat) was documented.

#### **Cape Fur Seal (*Arctocephalus pusillus*)**

Some time between 1825 and 1844, a half million Cape Fur Seals apparently died (Wyatt, 1980), though this figure is highly uncertain. Further, no data are available on the population size of the species at the time of harvest, although the overall population level of the Cape Fur Seal was very low at the end of the 19th century (Shaughnessy, 1984). The cause of this event is uncertain; however, it is thought that the die-off resulted from biotoxin poisoning resulting from red tide, or starvation due to mass mortality of fish. A similar event was reported in 1994; 100 000 animals apparently died of starvation resulting from the disappearance of fish stocks following an intrusion of an anoxic water mass onto the continental shelf (Anselmo *et al.*, 1995). The precise percentage of the population that was affected is unknown for both the 1825 and 1994 events.

#### **Antarctic Fur Seal (*Arctocephalus gazella*)**

Interannual variation in the availability of a primary prey item, krill, is thought to cause fluctuations in pup production at South Georgia (Croxall *et al.*, 1988; Boyd, 1993). Lactating females feed exclusively on krill, which may be absent in some years. Pup production in 1990–91 was reduced as a result of decreased local availability of prey, from an expected value of 378 000 to 269 000 (Boyd, 1993). As indicated by the duration of foraging trips, repro-

ductive performance fluctuated between 1983 and 1992 in response to food availability (Lunn *et al.*, 1994). In addition to influencing the foraging behaviour of adult females, interannual variability in krill abundance was found to influence the efficiency of the transfer of resources to pups, the age of first reproduction, the sex ratio of pups, and the date of parturition (Croxall & Prince, 1979).

Interannual variation in krill abundance had similar effects on Fur Seals on South Georgia between 1984 and 1990. Pup weight and mass at weaning decreased, and females made fewer but longer foraging trips in years of decreased krill abundance (Lunn *et al.*, 1993).

Also reported on South Georgia was a population-level effect of entanglement in man-made debris; an estimated 1% of animals had neck collars of man-made debris, and 30% of animals were found to be injured by such debris (Croxall *et al.*, 1990).

#### **Steller's Sea Lion (*Eumetopias jubatus*)**

Between 1960 and 1994, the Western population of Steller's Sea Lions declined by approximately 64% (NMFS, 1995). Possible causes include natural factors such as predation, disease, variation in abundance and distribution of prey, and other types of environmental change; nutritional stress caused by removal of prey by commercial fisheries; direct kills of sea lions by commercial and subsistence harvesting; intentional and incidental kills by fisheries; entanglement in marine debris; pollution; and other disturbances (NMFS, 1992). While there now seems to be general agreement that juvenile sea lions are suffering from nutritional stress (NMFS, 1995), there is still considerable uncertainty about the sources of that stress (NMFS, 1992).

#### **California Sea Lion (*Zalophus californianus californianus*)**

El Niño events appear to have a significant impact on California Sea Lion populations. On San Nicolas Island in California, the number of females decreased by 40% in 1983 and recovered to only 74% of the 1982 value in 1984 (DeLong & Antonelis, 1991). Decreased female fecundity and prolonged weaning were also reported (Francis & Heath, 1991). The effect on subadults remains unclear; however, a decrease in juvenile survival and a 30–70% reduction in pup production were reported in 1984 (DeLong & Antonelis, 1991; Francis & Heath, 1991). Pup numbers declined between 1982 and 1984 as a result of decreased copulation frequency and increased abortion rates. While no data exist on actual causes of pup mortality during this period, lower pup weights in 1983 indicate poor nutrition.

The US population of California Sea Lions has experienced several leptospirosis outbreaks, but the population-level effect of such outbreaks is unknown. In 1970, 315 animals became stranded, of which 125 died (Vedros *et al.*, 1971; Dierauf *et al.*, 1985). In 1984, 226 stranded animals were 'rescued', 66 of which were treated successfully (Dierauf *et al.*, 1985). A mass stranding event in 1947 is thought to have been caused by a leptospirosis outbreak; 'increased numbers of stranded animals diagnosed as bacterial pneumonia . . . leptospirosis cannot be ruled out' (Vedros *et al.*, 1971). In 1969–70, the abortion rate increased threefold over the 1969 rate on San Nicolas Island; it is thought that this change resulted from leptospirosis (Vedros *et al.*, 1971).

In the Mexican Pacific population, a 45% reduction in the number of pups born in 1983 was reported as a result of El Niño (Auriolos & Le Boeuf, 1991).

#### **Galapagos Sea Lion (*Zalophus californianus wollebaekii*)**

As mentioned, the most severe impact of the 1982–83 El Niño event on pinnipeds occurred off the Galapagos Islands (Trillmich, 1985, 1987; Trillmich & Dillinger, 1991). For

Galapagos Sea Lions, the event caused increased adult mortality in 1983, greater than 50% mortality of juveniles in 1982, and a 100% die-off of pups in 1982 (compared to an average pup mortality of less than 10%). In 1983, pup production also decreased. The event has caused a local redistribution of sea lions and a slow recovery (Trillmich & Dillinger, 1991; Laurie, pers. comm. as cited in Trillmich & Dillinger, 1991).

#### **South American Sea Lion (*Otaria byronia*)**

An unknown agent caused significant population declines of South American Sea Lion populations between the 1930s and the 1970s (Carrara, 1954; Ximenez, 1976; Campagna *et al.*, 1992). In 1937, the Falkland Islands population of sea lions was estimated to include 400 000 animals (Hamilton, 1939); by 1965 the population had declined to fewer than 30 000 animals (Strange, 1972, 1979; Laws, 1973), representing a 93% decline in pup production in under 30 years. Harvest levels over this period do not account for this decline. It is possible that the effects of fisheries or the oil industry may have caused this decline.

A similar trajectory has been reported for the adjacent Argentinean population on Peninsula Valdes, possibly as a result of the oil industry or fisheries or of directed harvest. This population declined from 137 000 in 1938 to 18 000 in 1949 to 14 000 in 1975 (Ximenez, 1976). The population has now abandoned beach sites accessible to hunters and is restricted to rocky islets and other inaccessible spots (Campagna *et al.*, 1992).

#### **South American Fur Seal (*Arctocephalus australis*)**

In Peru, the 1982/1983 El Niño resulted in greater than 41% pup mortality of South American Fur Seals in 1982; an increase in adult mortality (no quantitative data available); a 50% decrease in pup growth rate in 1983; increased length of foraging trips; and a local redistribution of breeding and haulout sites (Majluf, 1991).

In 1997, 55 000 tons of crude oil were spilled by a Panamanian tanker 20 nautical miles south-west of Isla de Lobos, Uruguay (Ponce de Leon, 1997). Immediate effects in 1997 on South American Fur Seals included mortality of 4738 pups (33% of total), 154 adult females and 10 adult males.

### **DISCUSSION**

We found seven populations that have been reduced to small enough sizes that they were thought extinct or near extinct. Of these, six have recovered. In the absence of quantitative time-series data on the actual population sizes, it is not possible to use the formal methods of Liermann & Hilborn (1997) for calculating depensation in these populations. However, historical data reviewed in this paper suggest that population levels were, at maximum, a few hundred animals. Thus, we can hypothesize that depensation does not become important in otariids until populations are at least below a few hundred animals. In other cases where quantitative abundance data are available, as in marine fishes (Liermann & Hilborn, 1997) and Australian marsupials (Sinclair *et al.*, 1998), such depensation thresholds have been calculated.

There are several caveats associated with the historical records of extinction thresholds for otariids. First, most of the records about historical population estimates and time of extinction are not quantitative. Second, it is clear that some populations were mistakenly recorded as extinct, or were recolonized from a previously unknown segment of the population. Third, it is possible that undiscovered populations have historically gone extinct without notice. For example, it is likely that Northern Fur Seals bred along the west coast of North America and were extirpated without record. Thus, there may be more cases of populations not recovering from catastrophes than are documented in the literature.

What does emerge from the data is that otariids have recovered from very low numbers on many occasions. Assuming that a 'quasi-extinction' population level is equivalent to extinction will therefore probably overestimate the risk of extinction. A possible avenue for future research would be to model the dynamics of populations that were reduced to low numbers and have recovered without immigration from other populations with a hypothetical distribution for the lowest density obtained, and estimate how rates of increase decline at low densities.

The data summarized on the frequency of catastrophes provided a useful starting point for theoretical approaches to incorporate catastrophic stochasticity into viability models. It is interesting to consider the interaction of causal factors leading to catastrophic events and the probability of recovery. For example, the four El Niño-induced catastrophes are well documented and straightforward. While otariids are probably adapted to such environmentally induced catastrophes to a certain extent (Trillmich & Ono, 1991), the concern about species recovery should focus on changes in frequency of El Niño events. The two South American Sea Lion population declines are more questionable because much of the decline may be due to hunting and human interference; thus, these may not be unpredictable catastrophes by our definition. Declines in species due to direct human impacts should be readily reversible because, in theory at least, human interference could be halted allowing rapid recovery of populations.

The probability of detecting a catastrophe in the historical record obviously differs from population to population. For instance, in the case of the Hooker's Sea Lions we considered only the last 4 years, with standardized mark-recapture surveys, as years when a catastrophe would have certainly been detected. Our estimate of 0.25–2.1% for annual probability of a catastrophe spans the range of bounds that could be used in analyses of extinction risk for otariids. A survey of experts on each of the populations on estimating of the probability of detecting a catastrophe of >50% of the breeding population during the historical record would allow parameterization of equation 3. With an estimate of  $q$ , the range of probability of catastrophe would narrow, and our estimate of probability of catastrophe would probably be lower than 2.1%. For example, if a survey of experts revealed that there was a 15% probability of detecting a catastrophic event for the entire recorded history of the population, the rate of catastrophe would be 1%. More in-depth modelling approaches could also investigate the different levels of catastrophes identified in Fig. 1 rather than limiting analyses to those with >50% intensity. For example, Gerber *et al.* (1999) demonstrate an approach using time-series abundance data in a simple logistic model to compute the likelihood profile for frequency and intensity of catastrophes.

We have demonstrated that it is possible to estimate the frequency of catastrophic events from the published literature for at least one taxonomic group. Much more remains to be done: there is obviously uncertainty over which cases to include as catastrophes, what denominator to use in calculating the frequency, and the spatial extent of catastrophes. However, given the importance of catastrophes in calculating extinction risk, it would seem imperative that an analysis such as that performed in this paper be an integral part of any analysis of extinction risk.

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